Smelling the goodness: sniffing as a behavioral measure of learned odor hedonics

Article (Accepted Version)

Smelling the goodness: sniffing as a behavioral measure of learned odor hedonics.

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Abstract

Pairing an odor and taste can change ratings of the odor's perceptual and hedonic characteristics. Behavioral indices of such changes are lacking and here we measured sniffing to assess learned changes in odor liking due to pairing with sweet and bitter tastes. Participants were divided on their liking for sweetness, as well as dietary disinhibition (TFEQ-D scale), both of which influence hedonic odor-taste learning. In sweet likers, both sniff duration and peak amplitude increased for the sweet-paired odor. Sniff magnitude decreased for sweet- and quinine-paired odors in sweet-dislikers, and sweet likers smelling the quinine-paired odor. In sweet-likers, liking for the sweet-paired odor increased with both TFEQ-D score and hunger, and sniff magnitude with TFEQ-D only. There were no predictors of changes in response to the quinine-paired odor. Brief co-experience of odors with sweet tastes can lead therefore to measurable changes in sniffing, providing a novel behavioral index of odor liking.

Keywords: Odor, taste, learning, sniffing

Introduction

Perception of flavor is a multi-sensory experience combining gustation, olfaction and somatosensation (Small & Prescott, 2005; Spence, 2013). One unexpected consequence of the co-experience of odors sensed retronasally with tastes in the mouth together as flavors is the subsequent attribution of taste characteristics to these odors when subsequently sniffed. Thus, odors co-experienced with sweet tastes subsequently smell sweeter (Stevenson, Boakes, & Prescott, 1998; Stevenson, Prescott, & Boakes, 1995; Yeomans, Mobini, Bertenshaw, & Gould, 2009a; Yeomans, Mobini, Elliman, Walker, & Stevenson, 2006), odors paired with sour tastes (citric acid) smell more sour (Stevenson et al., 1998; Stevenson, Boakes, & Wilson, 2000b; Stevenson et al., 1995), and odors paired with bitter (quinine) subsequently smell more bitter (Yeomans & Mobini, 2006; Yeomans et al., 2006). These experiences can also affect liking for odors: odors paired with sweet tastes become more liked provided participants liked the sweet taste (Yeomans & Mobini, 2006; Yeomans et al., 2006; Zellner, Rozin, Aron, & Kulish, 1983), while liking decreases for odors paired with disliked sour (Stevenson, Boakes, & Wilson, 2000a) or bitter (Yeomans & Mobini, 2006; Yeomans et al., 2006) tastes. These acquired taste qualities of odors have been interpreted as synesthesic experiences (Stevenson et al., 1998; Stevenson & Tomiczek, 2007), and appear resistant to extinction (Stevenson et al., 2000b). These surprising changes in odor perception through associations with tastes raise fundamental issues in perception, implying that learning as well as the odorant molecules determines odor quality.

The interpretation of studies looking at odor-taste associations typically relies on subjective self-report ratings of odor characteristics, and this has raised some concerns. In particular, apparent changes in odor perception might reflect changes in odor hedonics, since ratings of hedonics and sensory properties are not independent (Prescott, Lee, & Kim, 2011). This has been repeatedly shown in studies looking at how the addition of odors altered taste

intensity. For example, when participants rated the intensity of a sweet solution (aspartame), or a combination of aspartame and an odor (strawberry), the presence of the odor increased rated sweetness. However, when ratings of strawberry flavor and sweetness were included the apparent enhancement of sweetness by odor was much less (Frank, van der Klaauw, & Schifferstein, 1993).

A further issue for odor-taste studies with sweetness is the colloquial use of the word "sweet" has hedonic connotations. If participants were misinterpreting sweet in this way then this confounds attempts to separate hedonic and sensory changes for odors after odor-taste training. What then is needed is a methodology that can potentially reliably distinguish hedonic from sensory changes.

Recently it has been shown that the way that a participant engages with (sniffs) an odor varies depending on odor characteristics (Prescott, Burns, & Frank, 2010): the duration of sniffing was longer, and the maximum sniff strength greater, when people sniffed pleasant rather than neutral or unpleasant odors. That study used 17 test odor stimuli, including food-related and non-food odors, and relied on individual past experiences with the test odors. Applying the same methodology to examine changes in odor sniffing after odor-taste training provides a potential implicit measure of changes in odor perception, moving away from reliance on ratings alone.

One complication in interpretation of the outcome of past studies of odor-taste learning, particularly where sweetness was the trained taste, is that whereas ratings of sweetness increased universally, changes in liking were much less consistent. The earliest studies found no evidence of altered rated sweet liking despite clear evidence of increased odor sweetness (Stevenson et al., 1998; Stevenson et al., 2000a; Stevenson et al., 1995). Subsequent research suggested that this partly reflected differences in hedonic evaluation of sweetness, with increased liking for sweet-paired odors in people who liked the trained sweet

taste, but decreases in those who disliked this stimulus (Yeomans et al., 2006). However, there remains considerable variation in changes in odor liking even amongst those who like sweet tastes.

In this context, an intriguing finding is that personality traits may mediate the relationship between odor-taste learning and sweet liking. Women who were sweet likers and who scored highly on a measure of the extent to which they were prone to opportunistic eating (the disinhibition scale of the Three Factor Eating Questionnaire: TFEQ-D, Stunkard & Messick, 1985) showed much greater increases in liking for sweet-paired odors than did women who were also sweet likers but who scored lower on TFEQ-D (Yeomans et al., 2009a). The role of sweet taste as a driver of over-consumption is the focus of considerable debate in the context of the current worldwide increase in obesity (Bellisle, Drewnowski, Anderson, Westerterp-Plantenga, & Martin, 2012; Drewnowski, Mennella, Johnson, & Bellisle, 2012; Popkin, Bray, & Hu, 2014), and our earlier odor-taste study could imply that differences in the extent to which liked sweet tastes are individually rewarding may be key. Certainly, individual differences in response to food cues have been identified as risk factors for weight gain (Wardle, 2007), and notably TFEQ-D scores correlate positively with body-size (Hays & Roberts, 2008; Lawson et al., 1995). Women scoring high on TFEQ-D may seek hedonic rewards as a means of affect regulation (Wilkinson, Rowe, Bishop, & Brunstrom, 2010), and this could underlie their enhanced sensitivity to odor-sweet learning. We therefore also tested whether individual differences in odor-sweet associations were evident with a behavioral measure (sniffing) as well as odor ratings.

The overall aims of the study were thus twofold. Firstly we tested whether repeat co-experience of odors with sweet and bitter tastes altered the way participants subsequently sniffed these odors as a novel behavioral test of odor-taste learning. Secondly, we tested whether any effects of odor-taste training on sniffing and evaluating odors varied depending

on TFEQ-D scores as a measure of individual differences in sensitivity to sweet-based reward.

Method

Design

Changes in both the rated sensory and hedonic characteristics of odor stimuli and the way these odors were sniffed were assessed within-participant after pairing odors with either a sweet taste (sucrose), bitter taste (quinine) or water (control). The extent to which these changes depended on individual tendency to display opportunistic eating was assessed using regression analyses of the changes in response to the target odors as a function of scores on the TFEQ-D measure.

Participants

The test sample comprised 84 volunteer women, with an average age of 22 years (SD: 4 years), recruited from staff and students at the University of Sussex. The sample size was based on power analysis of data from our earlier study (Yeomans et al., 2009a): to replicate the reported relationship between TFEQ-D and change in liking for an odor paired with sucrose by sweet likers was estimated to require 32 sweet likers (giving n = 68 total), but since our key variable was acquired changes in sniffing where we had no previous data we increased the sample to reduce the risk of a Type 11 error. A female only sample was used since men typically score lower than women on TFEQ restraint, and consequently including both men and women would have lead to a potential gender confound in analyses involving TFEQ. All volunteers were healthy, did not smoke and had not experienced respiratory infections in the week prior to testing. A written information sheet detailed potential ingredients which participants might be exposed to, and those with allergies or aversions to

these were excluded, as were sufferers from diabetes and those with a prior diagnosis of an eating disorder. Participants were paid £5 on completion of the study, following debriefing. The protocol was approved by the University of Sussex Science and Technology Cross-Schools Research Ethics Committee (C-REC) and was conducted in line with the British Psychological Society code of conduct, ethical principles and guidelines.

Sweet taste screening

The sweet-taste screening protocol was the same as that used successfully in previous studies in our laboratory (Mobini, Chambers, & Yeomans, 2007; Yeomans & Mobini, 2006; Yeomans et al., 2006). Participants were provided with four 10ml samples, two each of 100 g/L (10%w/v) sucrose and two of water, presented at room temperature in 20 ml shot-glasses. They rated each sample using 100-pt horizontal visual analogue scales for flavor pleasantness (on a scale from "Extremely unpleasant", scored 0, to "Extremely pleasant", scored 100) and sweetness (on a scale from "Not at all", scored 0, to "Extremely", scored 100) using Sussex Ingestion Pattern Monitor (SIPM 2.015, University of Sussex) software. The label for the dimension to be evaluated was displayed above the center of each line. Following on-screen instructions, participants held each solution in their mouth for five seconds before expectorating into a sterile container, and were instructed to rinse their mouth with water between solutions. There was a 10 second pause between trials. Participants who rated both 10% sucrose solutions greater than 60 on the pleasantness scale were classified as consistent sweet likers, and less than 40 as consistent sweet dislikers, and these participants progressed to the next stage. Of the 84 participants, 23 were defined as dislikers and 61 as likers. A further 19 women failed the screening either because both their evaluations of sweet liking fell between cut-off values (i.e. between 40 and 60: n = 5), or because they were inconsistent in their responses (n = 14).

Test odor stimuli

To maximize the chance of an association between the test odors and trained sweet/bitter tastes, odors were selected which were initially perceived as having low levels of the trained taste characteristics (sweet and bitter) and which were rated as relatively neutral in pleasantness. The odor stimuli used were rhubarb (International Flavours and Fragrances), yoghurt (International Flavours and Fragrances) and cranberry (International Flavours and Fragrances).

Odor evaluations

Two types of data were collected to assess participant's responses to the trained odors.

Sniffing test. Sniffing behavior was measured using the procedure described by Prescott et al. (2010), using a device originally developed for the Sniff Magnitude Test (SMT: Frank et al., 2006). To provide a consistent odor stimulus, a sample of each of the three test odor (1 g rhubarb, 1.5g yoghurt or 1.2g cranberry: amount adjusted to ensure similar odor intensity) had been pipetted onto a small ball (1g) of cotton wool and placed into individual PVC odor stimulus canisters labeled with a 3-digit number. Following instructions from the experimenter, participants picked up the relevant container and positioned it 1-2cm from the external nares. Sniffing was monitored using a bilateral nasal oxygen cannula placed at the external nares. The initial force of inhalation activated a pressure transducer that opened the top of the canister, making the odor available. As the pressure of each sniff fell below an adjustable threshold, the valve closed, which in turn blocked access to the odor (Frank et al. 2006). The air pressure of the sniff was sampled at 100 Hz and recorded as a change in ambient air pressure, expressed in millivolts (mV). To familiarize participants with

the procedure, they were first presented with an empty canister, and they sniffed from this three times, with verbal correction from the experimenter if the positioning of the canister was incorrect. Then the three test odors were sampled in random order and the process repeated. The experimenter was then present throughout to ensure the correct canister was selected for each trial and the sniffing test was completed accurately.

Odor ratings. Immediately after the sniffing test, participants completed a series of ratings of each odor using visual analogue scale presented using Sussex Ingestion Pattern Monitor software. For this test, 40ml samples of each odor solution were presented in 200ml plastic squeeze bottles using the same odor concentrations as in the sniff test. Participants were told to hold the bottle just below their nose and squeeze to release the odor. Each odor was rated in terms of how pleasant, sweet, bitter, fruity, familiar and intense they were using 100pt visual analogue scale with end-anchors in the form "Not at all [attribute]" and "Extremely [attribute]". Odor presentation and rating odor were both randomized.

Odor-taste training

The training (exposure) phase started immediately after completion of the orthonasal odor evaluations, and used a triangle-test disguised training method first described by Stevenson et al. (Stevenson et al., 1995) and subsequently used successfully in our laboratory (Yeomans & Mobini, 2006; Yeomans et al., 2009a; Yeomans et al., 2006). Here, participants were provided with a single tray with 15 lidded 150ml polystyrene cups, with straws protruding to allow each stimulus to be sampled, arranged as 5 rows of three cups. Each row was numbered (1-5) and the 3 cups in each row labeled A, B and C. Participants were instructed (by computer) to select one row at a time and were told that in each set of three, one stimulus would be different, either in terms of flavor quality or intensity, and that their task was simply to identify which of the three stimuli was the odd-one-out. Of the five rows,

two were the key training sets, one with the target odor paired with 10% sucrose (SUC) and the second with 0.01% quinine hydrochloride (QUIN), both prepared as solutions (w/v) in deionized water. For these trials the three stimuli were identical, and so offered a disguised way of presenting odor-taste pairings repeatedly without drawing attention to sensory or hedonic qualities. The remaining three rows were control stimuli, designed to further disguise the purpose of the study, in line with the original procedures used to evaluate this form of olfactory learning in humans (Stevenson et al., 1998; Stevenson et al., 1995), and consistent with other recent studies in this laboratory (Yeomans & Mobini, 2006; Yeomans et al., 2006). These trials were mixed with dummy trials using additional flavor stimuli where there was an obvious odd-one-out: water-vanilla-water (vanilla extract: Nielsen-Massey, NL), raisin-raisin-water (raisin flavor: International Flavours and Fragrances) and water-saline-saline (0.1% NaCl). Each block of testing cycled through these five sets of stimuli in random order, and four blocks of trials were completed in total meaning that each participant sampled the key odor-SUC and odor-QUIN stimuli 12 times. Participants were instructed to take as many sips of each stimulus in each set necessary to determine the odd-one-out, swilling their mouth with mineral water between each stimulus, and were told that the trials would be repeated four times, and so if they were unsure which was the odd one out on any one trial that they should guess. Participants were required to record their choice of odd-one-out for each trial by clicking on one of three response boxes on the computer screen in order to ensure they paid attention to the stimulus features. Responses on the filler trials was then checked to ensure participants were attending to the stimuli: analysis confirmed that all participants were correct on >90% of the filler trials, with most participants (62/84) correct o 100% of these trials. There was a 30 second delay between sampling of each set of three stimuli, and 15 minute break between the four blocks of training trials. Pairing of the three test odors with the two training taste stimuli was counterbalanced across participants, with

the unpaired odor acting as an unexposed control. The process was controlled by on-screen instructions (programmed used E-prime 1.2, Psychology Software).

Procedure

All testing was conducted between 1000h-1200h in small air-conditioned cubicles at the Sussex Ingestion Behaviour Unit at University of Sussex. Participants attended on two separate occasions at least one and no more than seven days apart. The first session involved completion of the consent procedures and the sweet-taste screening procedure, and lasted around 20 minutes. Participants who met the study criteria were then invited to return to complete the main testing session, which took around 90 minutes. Participants had been instructed to refrain from eating and to drink only water for the two hours prior to the main tests, and on arrival were required to rate their hunger and thirst using visual analogue scale administered using Sussex Ingestion Pattern Monitor software, disguised as a mood questionnaire, to allow hunger state to be included in data analysis (see e.g. Yeomans & Chambers, 2011; Yeomans & Mobini, 2006). They then completed the pre-training odor evaluations, first the sniffing test and then the odor ratings. Odor-taste training started immediately after the final odor rating. Post-training re-evaluation of the odors followed the same sequence as the pre-training evaluations with the exception that the blank odor canister was no longer used for the sniffing test. Once the final odor evaluation had been completed, participant age, height and weight were recorded, participants were debriefed and paid for their participation.

Data analysis

Since the focus was on changes in behavior following odor-taste pairing, analysis was focused on changes in key measures of response to the test odors. For the ratings data

(pleasantness, sweetness and bitterness of the test odors), change data were calculated by subtracting the baseline (pre-training) ratings from those made post-training for the sweet-paired, quinine-paired and control (untrained) odors. These change scores were then contrasted between conditions (sweet, quinine or control), with sweet-liker status (liker or disliker) as additional factor using 2-way repeated measures ANOVA. Bonferroni-protected contrasts were used to compare between conditions where effects were significant, and to test if changes in each condition were significantly different from zero. Since the numbers of dislikers was small, Bayes factors were calculated for liker/dislike contrasts to check whether lac of significance could result from lack of study power. We also contrasted baseline ratings between conditions and sweet liker/disliker groups to guard against spurious baseline differences confounding change data.

For the sniffing data, values for each of the two "sniffs" for each odor both pre- and post-training were averaged to give a single measure in each test condition. Three measures were derived from the output from the SMT system in line with earlier work (Prescott et al., 2010): the sum of all pressure measurements during a sniff as an estimate of sniff volume (hereafter referred to as Sniff magnitude), sniff duration and maximum pressure of each sniff. For the first measure there were large individual differences (range 10.7 – 175.1), although each individual tended to be consistent across trials. Since the focus was again on changes after training, rather than calculating absolute change, the difference in Sniff magnitude for each condition was expressed as the percentage change from baseline. Data for sniff duration and maximum pressure were less variable, and simple change scores were calculated for these variables. All sniff measures were then contrasted using 2-way repeated measures ANOVA with condition (sweet, quinine or control) and liker status (liker or disliker) as factors.

Since previous research noted that both individual differences in eating attitudes between participants (TFEQ-D: Yeomans et al., 2009a) and acute hunger state (Yeomans & Mobini, 2006) can influence changes in odors by pairing with sweet tastes, we also (a) tested whether those findings were replicated in the current data and (b) tested whether similar effects were seen with the sniffing measures. The focus here was on changes in perception and sniffing for the sweet paired odor, and since there were multiple potential predictors (TFEQ-D, TFEQ-R, hunger, age and BMI), initial analysis used multiple regression to assess which of these were significant predictors in both sweet likers and dislikers. ANCOVA was then used to test whether the differences in changes in sweet pleasantness and Sniff Magnitude seen between likers and dislikers was moderated by the two factors which had been shown to predict change in odor pleasantness (TFEQ-D and hunger). All analyses were conducted using SPSS version 22 for Macintosh.

Results

Since sweet-liker status was included in analyses, initially we contrasted key demographic data for the defined sweet liker and disliker groups to see if there were potential confounding differences that needed to be controlled for. As can be seen (Table 1) there were no significant differences between liker and disliker groups in age, relative bodysize (BMI), TFEQ-D or TFEQ-R (restraint), or hunger at test. By definition the groups differed markedly in liking for the taste of 10% sucrose. Baseline evaluations (both rated and sniffing data) of the odors in the three training conditions can be seen in Table 2. Two-way ANOVA with condition (SUC, QUIN or Control) and group (Liker versus Disliker) found no significant overall differences between odor conditions or any significant main effects or interactions involving liker groups on any of these measures: see Table 1 for the full statistical analysis. Average responses did suggest that dislikers tended to sniff less overall,

with slightly shorter average sniff duration and lower peak sniff, than did likers, however none of these effects came close to significance: Bayes factors for the liker-disliker differences in baseline sniffing all fell between 1-2, below the level which would suggest an effect had been missed.

Changes in evaluation of the target odors

The change in rated sweetness of the odors varied significantly between the three conditions as predicted ($F(2,164) = 9.42$, $p<0.001$, $\eta^2 = 0.10$), but neither the overall effect of sweet liker status or condition x liker interaction were significant (main effect of sweet liking, $F(1,82) = 1.06$, $p = 0.32$, $\eta^2 = 0.01$: liking x condition interaction $F(2,164) = 0.38$, $p = 0.69$, $\eta^2 = 0.01$). Sweetness (Figure 1A) increased significantly in the SUC condition ($t(83) = 4.94$, $p<0.001$: 95% confidence interval 6.5 – 15.3), and this change was significantly different from the changes seen in the QUIN ($t(83) = 4.47$, $p<0.001$: 95% confidence interval 7.9 – 20.6) and Control conditions ($t(83) = 2.84$, $p<0.01$: 95% confidence interval 2.8 – 16.2). The overall changes in QUIN and Control conditions did not differ from zero (QUIN $t(83) = 1.30$, $p = 0.20$: Control, $t(83) = 0.61$, $p = 0.54$) and these two conditions did not differ significantly ($t(83) = 1.43$, $p = 0.16$: 95% confidence interval -3.4 – 13.0). Bayesian analysis of the liker/dislike difference confirmed there was no evidence of a group difference (Bayes factor = 1.0).

The change in rated bitterness of the odors also varied significantly with condition ($F(2,164) = 5.31$, $p=0.005$, $\eta^2 = 0.06$) but not liker status (main effect of sweet liking, $F(1,82) = 1.12$, $p = 0.29$, $\eta^2 = 0.01$: liking x condition interaction $F(2,164) = 0.02$, $p = 0.98$, $\eta^2 = 0.01$). The Bayes factor (1.0) for effects of liking group was consistent with a lack of difference. The bitterness of the QUIN-paired odor increased similarly in likers and dislikers (Figure 1B), and the overall change in bitterness was significantly greater than zero ($t(83) =$

4.12, p<0.001: 95% confidence interval 4.0 – 11.5) and significantly different from the equivalent changes in SUC (t(83) = 2.94, p=0.004) and Control (t(83) = 2.51, p=0.014) conditions, neither of which changed significantly from zero (SUC t(83) = 0/69, p = 0.49: Control, t(83) = 0.31, p = 0.76).

In contrast, changes in the rated pleasantness of the odors depended on both liker group ($F(1,82) = 12.27$, $p < 0.001$, $\eta^2 = 0.13$) and condition (liking x condition interaction $F(2,164) = 3.66$, $p = 0.03$, $\eta^2 = 0.04$). The only condition where rated pleasantness increased significantly from baseline was when sweet likers re-evaluated the sweet-paired odor (t(60) = 4.57, p<0.001: 95% confidence interval 5.6 – 14.3: see Figure 1C): in contrast pleasantness decreased significantly for the sweet-paired odor in the sweet dislikers ((t(22) = 4.22, p<0.001: 95% confidence interval -22.2 – -7.6). Odor pleasantness decreased significantly in both groups in the QUIN condition (likers t(60) = 3.19, p=0.002: dislikers (t(22) = 2.53, p=0.019), but although the decrease appeared to be greater in the disliker group, this was not significant (t(83) = 1.32, p=0.19, Bayes factor 1.0). Odor pleasantness did not change significantly in the Control condition in either group (likers t(60) = 0.48, p=0.63: dislikers (t(22) = 0.45, p=0.65).

Changes in measures of sniffing

Changes in Sniff Magnitude were similar in pattern to the data for rated odor pleasantness (Figure 2A), depending on liker group ($F(1,82) = 6.83$, $p = 0.011$, $\eta^2 = 0.08$) and condition (main effect, $F(2,164) = 6.30$, $p = 0.002$, $\eta^2 = 0.07$: liking x condition interaction $F(2,164) = 8.42$, $p < 0.001$, $\eta^2 = 0.09$). For the likers, the change in Sniff Magnitude varied significantly between the three conditions ($F(2,120) = 23.58$, $p<0.001$, $\eta^2 = 0.28$), with a significant increase in Sniff Magnitude relative to baseline only in the SUC condition (t(60) = 3.63, p<0.001, 95% confidence interval 5.9 %– 20.4%) and a significant decrease in Sniff

Magnitude relative to baseline in the QUIN condition ($t(60) = 5.96$, $p<0.001$, 95% confidence interval -22.8% - 11.3%). The change in the Control condition did not differ from zero ($t(60) = 0.43$, $p=0.67$) and differed significantly from the other two conditions (SUC: $t(60) = 3.98$, $p<0.001$: QUIN $t(60) = 3.34$, $p=0.001$). In contrast, Sniff Magnitude decreased in all three conditions for Sweet Dislikers, with no significant difference between these there conditions ($F(2,44) = 0.16$, $p=0.85$, $\eta^2 < 0.01$). These changes in Sniff Magnitude were a product of changes in both sniff duration and peak sniff amplitude after training (Figures 2B/C). As with Sniff Magnitude, changes in Sniff Duration differed between liker groups ($F(1,82) = 6.39$, $p = 0.013$, $\eta^2 = 0.07$) and although the overall effect of condition was not significant ($F(2,164) = 1.38$, $p = 0.25$, $\eta^2 = 0.02$), the liker x condition interaction was ($F(2,164) = 4.98$, $p = 0.008$, $\eta^2 = 0.06$). As with Sniff Magnitude, there was no significant difference in Sniff Duration between conditions in the Sweet Dislikers ($F(2,44) = 0.54$, $p=0.59$, $\eta^2 = 0.02$), with a similar decrease in all three conditions. For the likers, as with Sniff Magnitude, Sniff Duration varied significantly between conditions ($F(2,120) = 10.09$, $p<0.001$, $\eta^2 = 0.14$: Figure 2B). However, the only significant change from baseline was a significant decrease in the QUIN condition ($t(60) = 5.76$, $p<0.001$, 95% confidence interval -0.19 – -0.9sec), significantly different to the changes in SUC ($t(60) = 3.93$, $p<0.001$) and Control conditions ($t(60) = 2.69$, $p=0.008$). There was also a significant overall difference between liker groups in peak sniff ($F(1,82) = 6.75$, $p = 0.011$, $\eta^2 = 0.08$: Figure 2C), which also varied with condition ($F(2,164) = 3.11$, $p = 0.047$, $\eta^2 = 0.04$), but the interaction was not significant ($F(2,164) = 2.28$, $p = 0.10$, $\eta^2 = 0.03$). Peak Sniff decreased significantly relative to baseline in all three conditions in dislikers (SUC $t(22) = 2.87$, $p=0.008$: QUIN $t(22) = 3.12$, $p=0.005$: Control $t(22) = 2.71$, $p=0.013$) but the only significant change from baseline in the likers was a decrease in the QUIN condition ($t(60) = 5.05$, $p<0.001$), with no significant change in SUC ($t(60) = 1.78$, $p=0.08$) or Control conditions ($t(60) = 1.00$, $p=0.32$).

Predictors of changes in responses to odors

Neither age, BMI or TFEQ-R were significant predictors of either changes in pleasantness, sweetness, bitterness or Sniff Magnitude for the SUC-paired odor in either likers or dislikers. These regression did find that change in the pleasantness increased with TFEQ-D score (Figure 3A: Beta = 0.40, $t(60) = 3.08$, $p = 0.003$) and with hunger (Figure 3B: Beta = 0.28, $t(60) = 2.60$, $p = 0.012$) for the SUC paired odor when assessed by sweet likers. TFEQ-D score and hunger were not significantly correlated ($r = 0.23$, $p = 0.07$). No such effects were seen for changes in odor sweetness (TFEQ-D: Beta = 0.01, $t(60) = -0.01$, $p = 0.99$: hunger, Beta = -0.12, $t(60) = -0.87$, $p = 0.39$) or bitterness (TFEQ-D: Beta = 0.09, $t(60) = 0.59$, $p = 0.56$: hunger, Beta = 0.07, $t(60) = 0.53$, $p = 0.60$). TFEQ-D was the only significant predictor of changes in Sniff Magnitude for the sweet-likers (Figure 3C: Beta = 0.48, $t(60) = 3.42$, $p = 0.001$): effects of hunger were not significant (Beta = -0.10, $t(60) = -0.82$, $p = 0.42$). In contrast, neither TFEQ-D or hunger were significant predictors of the changes in odor pleasantness (TFEQ-D: Beta = 0.07, $t(23) = 0.21$, $p = 0.84$: hunger, Beta = 0.03, $t(23) = 0.12$, $p = 0.91$), sweetness (TFEQ-D: Beta = 0.07, $t(23) = 0.21$, $p = 0.84$: hunger, Beta = 0.03, $t(23) = 0.12$, $p = 0.91$) or bitterness (TFEQ-D: Beta = 0.07, $t(23) = 0.21$, $p = 0.84$: hunger, Beta = 0.03, $t(23) = 0.12$, $p = 0.91$) in the sweet disliker group. When the influence of TFEQ-D on changes in pleasantness and Sniff Magnitude in the SUC condition between likers and dislikers were contrasted using ANCOVA, the interaction between liker status and TFEQ-D was significant (pleasantness, $F(1,80) = 9.31$ $p<0.001$, $\eta^2 = 0.10$): Sniff Magnitude, $F(1,80) = 6.57$ $p=0.012$, $\eta^2 = 0.08$). In contrast, ANCOVA found no significant difference in impact of hunger state on changes in odor pleasantness or Sniff Magnitude between likers and dislikers (pleasantness, $F(1,80) = 1.72$ $p=0.19$, $\eta^2 = 0.02$): Sniff Magnitude, $F(1,80) = 2.16$ $p=0.15$, $\eta^2 = 0.03$).

There were no significant predictor of changes in response to the quinine-paired odor in either sweet likers or dislikers, suggesting the acquired dislike and consequent tendency for reduced engagement with the odor after training was independent of hunger state or other predictors.

Discussion

The present study is the first report of learned changes in how odors are sniffed, and provides clear evidence that these behavioral responses are guided primarily by hedonics. In doing so, the study clearly dissociates perceptual (odor intensity) and hedonic responses to odors since the pattern of sniffing matched that for changes in hedonic but not sweetness evaluations. This counters suggestions that apparent changes in the perceptual characteristics of odors after association with tastes are an artifact of hedonic change: here perceptual and hedonic changes were clearly dissociable both in the rating and sniffing data. Finally, the present data suggest that individual differences in sniffing for sweet-paired odors depend both on individual sweet liking and also scores on TFEQ-D.

The amount of odor that was sniffed provided a novel behavioral measure of liking: sweet likers, but not dislikers, increased both their liking for an odor paired with the sweet taste of 10% sucrose, and an estimate of the amount of odor inhaled (Sniff magnitude). In contrast, sweet dislikers decreased liking and sniffed less of the odor after training, a pattern of response seen for all participants when testing the odor they had paired with the disliked bitter taste of quinine. Thus odor-taste training clearly modified the degree of engagement with odors, and this fits with broader ideas about the adaptive purpose of sniffing (Hoover, 2010). Since humans and other animals have to learn which sources of nutrients are safe (Yeomans, 2006), associations between the odor characteristics of nutritive foods and rewarding aspects of ingestion such as sweet tastes or nutrient content provide a signal that

can subsequently aid location of these foods in the environment. Sweet taste preferences are hypothesized to have evolved because sweetness predicts the presence of sugar (Drewnowski, 1997; Ventura & Mennella, 2011). Accordingly, engaging more strongly with odors predicting a rewarding sweet taste makes adaptive sense, explaining the increased odor intake by sweet likers for sucrose-paired odors. Likewise, avoidance of an odor that is associated with a disliked taste can be interpreted as an adaptive response by helping avoid potentially harmful stimuli, evidenced by reduced sniffing for malodors (Frank, Dulay, & Gesteland, 2003). However, the sniffing behavior of sweet likers and dislikers did show differences in the extent to which hedonics aligned with changes in sniffing. For likers, the similarity between liking change and sniffing change was clear: for dislikers, where liking for both SUC and QUIN paired odors decreased, the finding that Sniff Magnitude also decreased in the Control condition suggests sniffing was less a direct reflection of acute hedonic evaluation in that group. It may be that for sweet dislikers, the experience of aversive stimuli only during training (since they disliked sucrose) was influential, resulting in a general avoidance of all odors post-training. This does not detract from the clear correspondence between hedonics and sniffing in likers, but suggests that sniffing may also be influenced by factors other than hedonics which would need both further investigation and some caution before sniffing was more widely used as a behavioral measure of changes in responses to odors by association with tastes.

What is curious, and remains obscure, is the clear dislike for sweet tastes by a subset of the population tested here, the disliker group in this and earlier studies (Dichter, Smoski, Kampov- Polevoy, Gallop, & Garbutt, 2010; Kim, Prescott, & Kim, 2014; Looy, Callaghan, & Weingarten, 1992; Looy & Weingarten, 1992; Pangborn, 1970; Yeomans et al., 2006; Yeomans, Tepper, Rietschel, & Prescott, 2007). What then underlies this dislike for sweetness? Previously we and others explored whether sweet disliking was a consequence of a well-known genetic variability in taste sensitivity indexed by taste responses to the bitter agent propylthiouracil (PROP) (Looy & Weingarten, 1992; Yeomans et al., 2007). Sweet

dislikers were more likely to be PROP supertasters, and had more fungiform taste papillae, but these effects could not fully account for sweet disliking. An odor-taste learning study with the artificial sweetener saccharin as paired tastant confirmed that changes in odor liking were related to individual liking for saccharin, and that even though more PROP super-tasters were sweet dislikers, PROP taster status did not predict the hedonic change through pairing with saccharin (Yeomans, Prescott, & Gould, 2009b). Thus sweet disliking does not appear to be explained purely as a difference in peripheral sensing of sweet taste, but more in terms of the extent to which this sensed taste is individually rewarding. There is also surprisingly little published data on the relationship between sweet liking and actual food use, but what there is suggests laboratory measures of sweet liking do relate to real sugar use: sweet likers tended to consume more sugar overall than did dislikers (Methven, Xiao, Cai, & Prescott, 2016), while sweet liking was associated with preferences for sweetened breakfast cereals (Mennella, Lukasewycz, Griffith, & Beauchamp, 2011) and higher liking for sweet foods in general (Kim et al., 2014). However, the nature of sweet disliking remains unclear.

Alongside clear differences in response of sweet liker and disliker groups, changes in odor liking and sniffing by sweet likers were further predicted by scores on TFEQ-D, replicating our earlier study (Yeomans et al., 2009a). Sniffing thus provided a novel behavioral measure of sensitivity to rewarding effects of sweet tastes, and notably increased sniffing for the sweet-paired odor as a function of TFEQ-D was independent of actual rated liking or perceived sweetness of the trained sweet taste. Thus high scorers on TFEQ-D do not express higher liking per se, but rather seem to find liked stimuli more rewarding.

The adaptive value of sniffing is evident in its responsiveness to motivational state: hunger produces longer and stronger sniffing (Prescott et al 2010). Similarly, expression of liking for an odor paired with sweet tastes in sweet likers depended on acute hunger state, with lower acquired liking when participants had been sated prior to odor re-evaluation

(Yeomans & Mobini, 2006). Here we did not explicitly manipulate hunger state, but rated hunger at test did not predict changes in sniffing or rated odor liking. However, average rated hunger in the present study (60±4) was more similar to hungry (54±7) than sated (32±7) participants in our previous study (Yeomans & Mobini, 2006), and there may not have been sufficient individuals who were sated to uncover any influence of hunger state on sniffing behavior. Recent data do suggest hunger should influence sniffing: infusion of ghrelin, a hormone associated with increased hunger in humans (Cummings et al., 2001; Tschop et al., 2001), increased sniff magnitude without altering rated odor pleasantness for established food-related odors in human volunteers (Tong et al., 2011). Since responses to food-related odors are likely to be learned, an important future study should examine how manipulated satiety modifies sniffing for sweet-paired odors, and the extent to which any effects of satiety are driven through changes in ghrelin.

The study has a number of limitations that suggest further studies are needed to fully evaluate the potential use of sniffing as a behavioral measure of odor-taste learning. Firstly, we tested a sample of women only to control for gender differences in responses on the TFEQ measures. Although there is no reason to believe that men would behave differently, a follow up study using men and women would be helpful. Secondly, the study was powered by estimation of the numbers of sweet likers needed: the numbers classified as sweet dislikers was smaller, and there is some risk that some effects where no differences were seen between likers and dislikers may have been under-powered, although Bayesian analyses found no evidence that any of the reported non-significant liker-disliker contrasts raised concerns of Type 2 errors. We also note there was large variation in the size of "sniffs" between participants, and the use of percentage change values was used to accommodate this. Alternative approaches where data were transformed were also explored, with similar

outcomes, but the percentage change value seemed to best capture the notion of proportional changes in sniffing.

Conclusion

The present study provides the first evidence that brief co-experience of odors with sweet tastes can lead to measurable changes in sniffing of the odor in line with the hedonic evaluation of the sweet taste, providing a novel behavioral index of odor liking, particularly for sweet likers. This measure was sensitive to individual differences in both liking for sweet taste and tendency to overeat, indexed by TFEQ-H scores, and provides a new tool to further explore acquired motivation to overeat in humans.

Author Contributions

Both authors contributed to the concept for the study and the final design. Testing and data collection were performed under the supervision of M.R Yeomans. M.R. Yeomans performed the data analysis and both authors contributed to data interpretation. M.R. Yeomans drafted the manuscript, and J. Prescott provided critical revisions. Both authors approved the final version of the manuscript for submission.

Acknowledgements

The authors wish to thank Sinitta Akaraskul for her assistance with data collection, and International Flavours and Fragrances for the donation of the odor stimuli used in this study.

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Table 1. Demographic characteristics, hunger at test and actual liking for the trained sweet taste of the defined sweet liker and sweet disliker groups. All values are mean ± SEM

	Likers (n = 61)	Dislikers (n = 23)	t(92)
Age (years)	21.7 ± 0.5	22.0 ± 3.9	0.31
BMI (kg/m^2)	22.3 ± 2.3	23.1 ± 2.9	1.22
TFEQ – D	6.1 ± 4.1	5.1 ± 4.0	0.95
TFEQ – R	8.1 ± 5.1	7.8 ± 4.5	0.20
Hunger	59.9 ± 3.8	54.9 ± 7.1	0.67
Liking for 10% sucrose	80.0 ± 1.5	22.3 ± 2.2	20.81, ***

Table 2. Analysis of the baseline hedonic and sensory ratings, and sniffing measures, for the odors in the three conditions for sweet liker and sweet disliker groups. All values are mean ± SEM, likers n = 61, dislikers n = 23.

		Training condition			Outcome of 2-way ANOVA		
Odor characteristic	Liker/disliker group	Sucrose	Quinine	Control	Main effect of condition	Main effect of Liker group	Condition x liker interaction
Pleasantness (100 pt VAS rating)	Liker	48 ± 3	47 ± 3	45 ± 3	$F(2,164) = 0.02$, $p = 0.98$, $\eta^2 < 0.01$	$F(1,82) = 0.07$, $p = 0.79$, $\eta^2 < 0.01$	$F(2,164) = 0.15$, $p = 0.86$, $\eta^2 < 0.01$
	Disliker	45 ± 4	47 ± 5	52 ± 5			
Sweetness (100 pt VAS rating)	Liker	44 ± 3	45 ± 4	42 ± 3	$F(2,164) = 0.35$, $p = 0.70$, $\eta^2 < 0.01$	$F(1,82) = 0.01$, $p = 0.94$, $\eta^2 < 0.01$	$F(2,164) = 1.63$, $p = 0.20$, $\eta^2 = 0.02$
	Disliker	47 ± 5	41 ± 6	49 ± 5			
Bitterness (100 pt VAS rating)	Liker	30 ± 3	28 ± 3	30 ± 3	$F(2,164) = 0.01$, $p = 0.99$, $\eta^2 < 0.01$	$F(1,82) = 0.01$, $p = 0.93$, $\eta^2 < 0.01$	$F(2,164) = 0.25$, $p = 0.78$, $\eta^2 < 0.01$
	Disliker	28 ± 5	31 ± 5	28 ± 4			
Sniff magnitude (mV)	Liker	51 ± 3	51 ± 4	50 ± 4	$F(2,164) = 0.15$, $p = 0.86$, $\eta^2 < 0.01$	$F(1,82) = 2.04$, $p = 0.16$, $\eta^2 = 0.02$	$F(2,164) = 1.06$, $p = 0.35$, $\eta^2 = 0.01$
	Disliker	41 ± 6	40 ± 6	43 ± 6			
Sniff duration (sec)	Liker	1.04 ± 0.07	1.00 ± 0.07	1.00 ± 0.07	$F(2,164) = 1.19$, $p = 0.31$, $\eta^2 = 0.01$	$F(1,82) = 2.17$, $p = 0.14$, $\eta^2 = 0.03$	$F(2,164) = 0.42$, $p = 0.66$, $\eta^2 = 0.01$
	Disliker	0.85 ± 0.11	0.79 ± 0.11	0.84 ± 0.12			
Peak sniff (mV)	Liker	0.51 ± 0.03	0.51 ±0.03	0.51 ± 0.04	$F(2,164) = 1.13$, $p = 0.33$, $\eta^2 = 0.01$	$F(1,82) = 1.52$, $p = 0.22$, $\eta^2 = 0.02$	$F(2,164) = 1.18$, $p = 0.31$, $\eta^2 = 0.01$
	Disliker	0.41 ± 0.05	0.44 ± 0.05	0.45 ± 0.06			

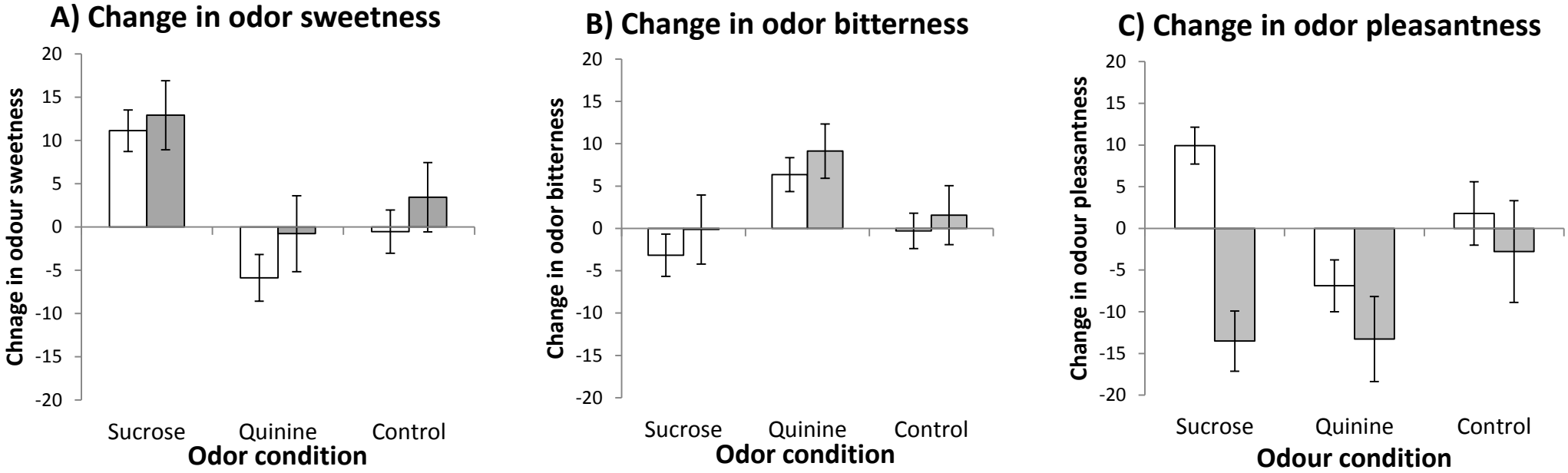

Figure 1. Changes in sweetness, bitterness and pleasantness of test odors following repeated pairing with a sweet (Sucrose) or bitter (Quinine) taste, along with an unexposed odor (Control), by participants pre-defined as sweet likers (open bars) or dislikers (filled bars). All data are mean ± SEM.

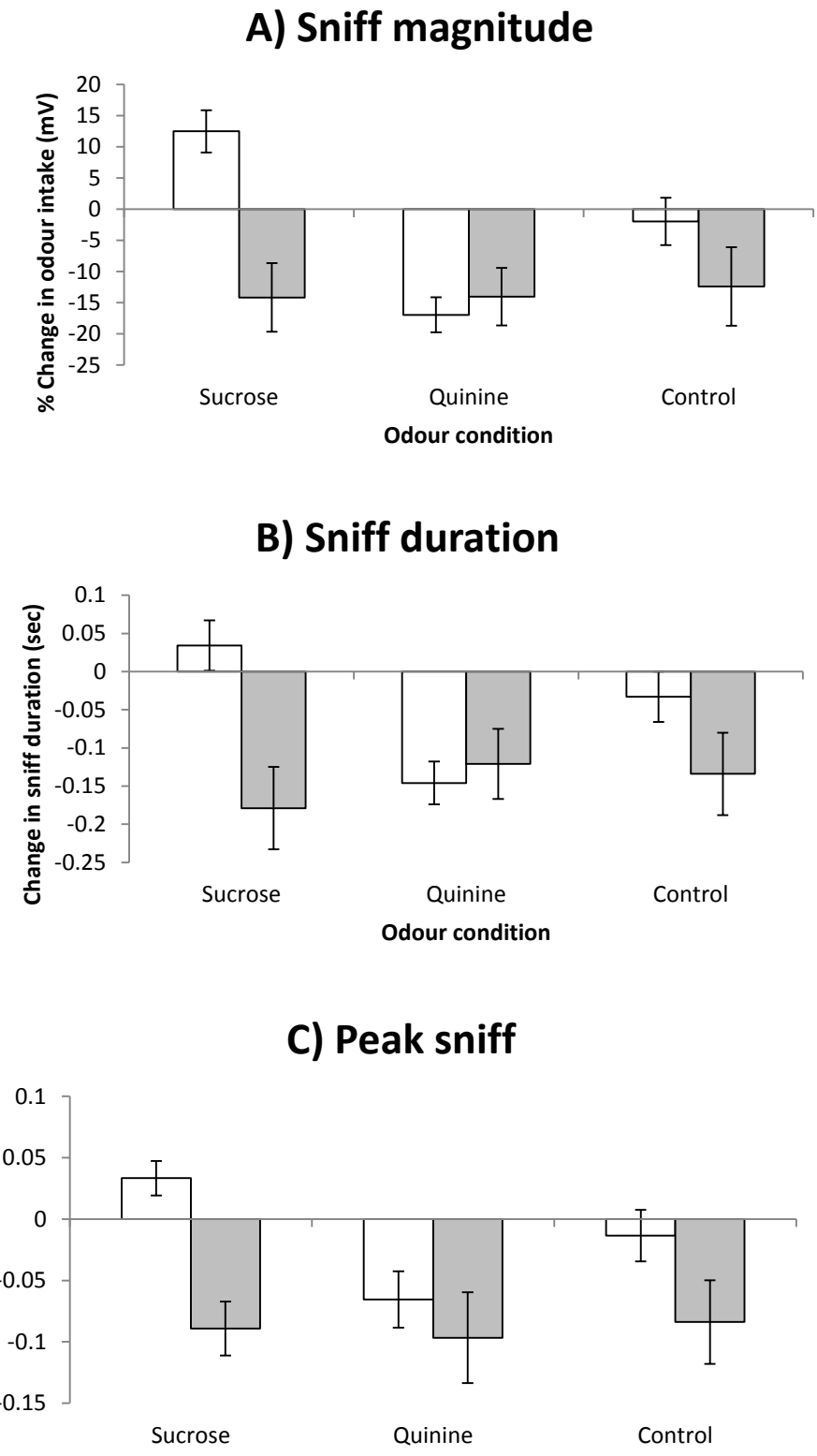

Figure 2. Changes in measured sniffing of test odors following repeated pairing with a sweet (sucrose) or bitter (quinine) taste, along with an unexposed odor (control), by participants pre-defined as sweet likers (open bars) or dislikers (filled bars). Data are (A) overall change in pressure (Sniff Magnitude), (B) sniff duration and (C) peak sniff. All data are mean ± SEM.

Figure 3. Individual predictors of changes in response to the sweet-paired odor. Data are (A) changes in pleasantness of the sweet-paired odor depending on scores on the TFEQ-D measure in likers (solid circles, solid line) and dislikers (open circles, dashed line), (B) changes in pleasantness of the sweet-paired odor depending on rated hunger at time of testing in likers (solid circles, solid line) and dislikers (open circles, dashed line), and (C) changes in Sniff Magnitude for the sweet-paired odor depending on scores on the TFEQ-D measure in